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AN ANATOMICAL STUDY OF GYMNOSPORANGIUM GALLS

ALBAN STEWART

GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE ON JUNIPERUS VIRGINIANA

The common "cedar apple" on *Juniperus virginiana* L., caused by *Gymnosporangium juniperi-virginianae* Schw., is one of our most common galls on coniferous plants. While the organism that causes this gall has been widely studied, but little work has been done on the changes brought about in the tissues of the host through the activities of this parasite, and the results obtained are contradictory.

Sanford (8) was the first one to investigate the anatomy of the cedar apple caused by *G. juniperi-virginianae*. He considers the gall to be formed by an abnormal growth of leaf tissue, which carries the apex of the leaf up as the gall develops, and pushes the branch bearing it to one side until the gall appears to be terminal. He further states that the vascular system enters the knot as one single bundle, given off from the vascular bundle of the branch of the tree, and further, that as the knot increases in size the vascular bundle develops rapidly until it appears like the vascular system of a branch.

Wörnle (11) who has done more work than any other investigator on the anatomy of Gymnosporangium galls, considers that the gall arises from a swelling of the stem induced by the fungus, that leaves may also enter into its composition, and, if dormant buds are encountered, they also may be stimulated to development.

Kern (6), who probably bases his statement on the work of Sanford, gives the cedar apple as an example of a gall originating in the leaves. Engler and Prantl (4), on the other hand, describe both *G. juniperi-virginianae* and *G. globosum* as causing woody galls on *Juniperus virginiana*.

Heald (5, pl. 10) has recently figured very young galls of this kind as arising near the axils of the leaves, and Coons (1, figs. 1 and 5) has figured galls some of which appear to be axillary in origin, and others arise from the upper surface of the leaf.

These rather conflicting statements in regard to the morphology of this gall seemed to offer an opportunity for further investigation. As the juniper trees in the vicinity of Madison, Wisconsin, furnished abundant material of this gall in various stages of development I concluded to determine, at least for my own satisfaction, which of these statements was correct. I soon discovered, from external examination, that some of the older galls had remains of more than one leaf attached to them, a fact which in itself would indicate that stem tissue was involved to a greater or less extent. I found still further, that normal branches are attached to the gall, apparently growing out from it at times (fig. 7), a condition that would be rather unusual if the gall were composed entirely of modified leaf tissue. Rather thick hand-sections showed that when a gall was located on the end of a stem, the stem continued into it for some distance before it broke up. This hasty examination seemed to justify a more careful study, the results of which are given in the following pages.

Before entering into the description of the anatomy of the gall it seems desirable to describe briefly the anatomy of both the leaf and young stem, as both of these are involved in gall formation.

The normal leaf is triangular in cross section except towards the base where it is rather four-sided. The epidermis is heavily cutinized and forms a smooth layer on the outer (morphologically lower) side of the leaf. Towards the edges and inner side, however, the individual cells are somewhat raised towards the outside causing them to appear more or less papilliform when seen under the microscope. The stomata occur mostly in the inner (morphologically upper) epidermis, but they may appear occasionally in the outer epidermis near the edges of the leaf.

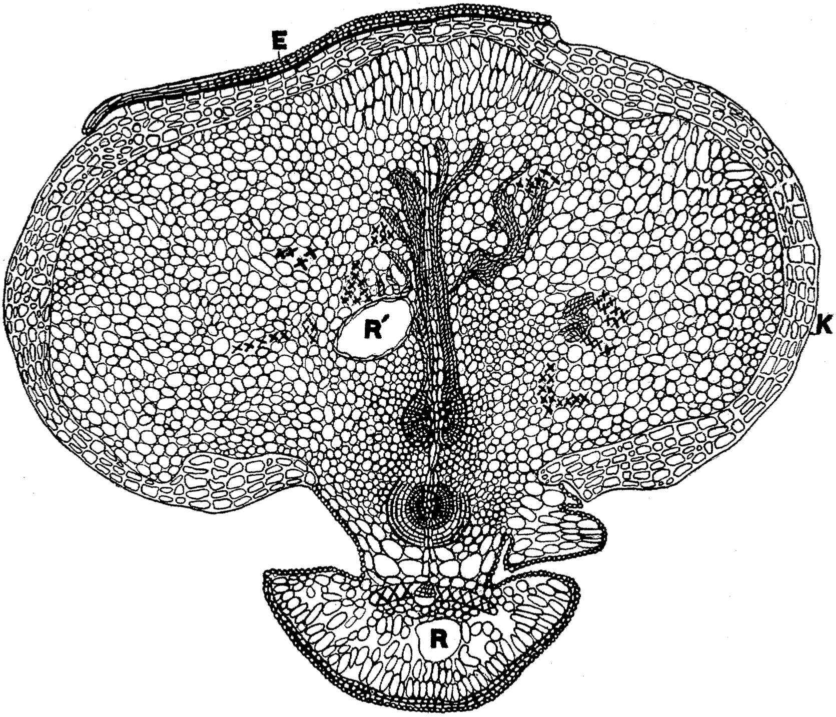
In addition to the epidermis, the outer side of the leaf is protected by a hypodermis which may extend entirely or only part way across this side. The hypodermal cells are usually arranged in one or two layers, although three layers may be present at times over a space. Sanford (8) describes a double epidermal layer for this side of the leaf but he evidently mistook the hypoderm for an inner epidermal layer. The interior of the leaf is filled with rather thin-walled parenchyma cells (text fig. 1) which are loosely arranged towards the inner side near where the stomata are borne, and resemble very much ordinary spongy leaf tissue. Towards the outer side of the leaf the parenchyma cells are elongated perpendicular to the surface and form a palisade tissue. The base of the leaf is united with the stem for some distance. A large resin cavity occurs in this region of the leaf. A single bundle enters the upper part of the leaf, xylem above and phloem below. On each side of this bundle are peculiar tracheids with bordered pits and bar-like thickenings (text fig. 1, xxx). For further consideration of these tracheids see De Bary (2).

It is sometimes difficult to determine in the young stem which of the cells belong to the leaf and which to the outer bark of the stem as the leaf and stem tissue blend together more or less at the point of union of leaf and stem. Between the attachment of the opposite leaves, however, the stem is exposed and is covered with epidermal cells similar to those which occur on the inner side of the leaf. There is a single layer of rather thick-walled parenchyma cells inside the epidermis, followed farther in by one or more layers of large, thin-walled, oval-shaped parenchyma cells. The inner bark is composed of concentric rings of bast fibers between each two of which there are three layers of cells. According to De Bary (2), two of these layers are of sieve tubes which are separated from each other by a layer of parenchyma cells.

The xylem of the young stem is composed of small triangular groups of tracheids, separated from similar adjacent groups by uniseriate rays. The rays extend outward into the inner bark, thus dividing the phloem and bast region into segments. The rays are broader opposite where the leaf trace bundles leave the xylem portion of the central cylinder. This broadening comes about usually by an enlargement of the ray cells, but sometimes there is an interpolation of additional ray cells. As two leaf traces leave the stem about opposite each other, the gaps caused by the broader rays divide the woody portion of the central cylinder into two nearly symmetrical halves. A small V-shaped depression occurs in the xylem where the leaf trace leaves it. A small group of pith cells occupies the center of the stem.

A diagrammatic drawing of a very young cedar apple gall and the stem that bears it is shown in figure 1. This gall has arisen from the axil of a leaf, a portion of which is shown to the right of the figure. I have examined a large number of young galls and have been unable to find any which were similar to the two figured by Coons (1, right side of fig. 1), which according to the figure have arisen evidently from the surface of the leaf. I have also been unable to find any young galls which were terminally located, and which might have arisen from the infection of a terminal bud such as has been suggested by Wörnle. They were always distinctly axillary in position although on the same tree with them there were older galls which were apparently terminal. According to Sanford (8), the branch is pushed to one side during the development of the gall. If this be true the terminal position of many of the older galls is probably more apparent than real.

The leaf, from the axil of which the gall arises, is pushed outward to some extent so that a small shelf is formed on which the gall rests. Apparently the fungus has not entered the stem at this stage as no abnormalities appear beyond a slight production of cork just above the gall (fig. 1). In the stage figured, the gall consists entirely of



TEXT FIG. 1. Semi-diagrammatic drawing of a cross section of a young gall of *Gymnosporangium juniperi-virginianae* and of the stem that bears it. Normal leaf shown below with resin cavity (*r*). Immediately above this is the central cylinder of the stem, and above this the central cylinder in the gall with its branches. *E*, epidermis and hypodermis of leaf; *K*, cork layer surrounding gall; *R′*, resin cavity in gall; × 42.

rows of parenchyma, which is covered on the outside by layers of cork cells (*k*). The leaf trace bundles are shown at *l*, two of which leave the woody cylinder (*c*), about opposite each other. Immediately above the leaf-trace bundle, on the right side of the figure, there is another bundle which is given off from the woody cylinder of the stem and extends to the base of the gall. Figure 2 is a diagrammatic drawing of a longitudinal section of a young stem and of an axillary bud (*bd*). Towards the lower part of the figure the central cylinder gives off two leaf-trace bundles (*l*), which go to a pair of opposite leaves. Just above the place of departure of the leaf-trace bundles, the central cylinder of the stem divides. One of the branches goes off to the right as a continuation of the stem, while the branch to the left enters the base of the young bud (*bd*). The similarity between figs. 1 and 2 is so great as to leave no doubt about the origin of the gall, as the vascular systems are the same in each case. The gall can be nothing more than an abnormally developed axillary bud, but whether or not it is a bud transformed I am unable to state definitely. It seems likely that the fungus has stimulated the development of a bud which from the start is transformed into a gall. I have examined a number of galls, in about the same stage of development as the one shown in figure 1, but have failed to find in any of them an indication of embryonic leaves, such as would probably be the case if the bud were already formed when the infection took place. In the witch's broom on this same species of juniper, caused by *Gymnosporangium juvenescens* Kern, the development of buds is greatly stimulated. It is not unreasonable to suppose that a somewhat similar condition exists here in regard to bud development.

After having considered to some extent a longitudinal section of the vascular system of a very young gall, it seems well to consider the cross section of a somewhat older gall and of the branch that bears it. Such a section is shown semidiagrammatically in text figure 1. A cross section of a normal leaf is shown in the lower part of the figure with a leaf trace bundle entering it. The leaf trace is flanked on each side by rows of tracheids with bar-like thickenings, shown by ××× in the figure. A portion of the base of another leaf is shown to the right, while the gall occupies the upper part of the figure. Just above the section of the lower leaf is the cross section of the stem that bears the gall. The heavy lines represent the rings of bast fibers, which are absent on the side next to the gall. Above the cross section of this stem there is still another, which in lower sections has all of the structures of a normal stem. There are triangular wedges of xylem, leaf gaps, rays somewhat broader than normal, and a pith. Surrounding this is a region of secondary bark tissue resembling the normal in many respects except that the bast rings are poorly developed. In the section drawn the woody portion of the cylinder has become more or less broken up and the cells turned over but it still preserves enough of the original structure to show that it is a stem. In place of secondary bark tissue there are small parenchyma cells instead. It should be noticed that a bundle leaves this modified stem on the upper side and extends into the gall. It is made up of two strands of scalariform tracheids, separated from each other the most of the way by a strand of parenchyma. This bundle is too large for a leaf-trace bundle, nor does it have the structure of such. It is more like that of a branch the central strand of parenchyma probably being the pith. Branches are given off from this which run an irregular course. These branches are composed of scalariform tracheids which often have groups of other tracheids with bar-like thickenings in connection with them shown by ××× in the figure. Groups of similar tracheids occur in other parts of the gall. The epidermis and hypodermis of the leaf is shown at *e*, on the upper side of the figure. This is the leaf from the axil of which the gall has arisen (see fig. 1) the tissue of which has become involved in the formation of the gall since the stage shown in the figure just mentioned. The gall is surrounded by several layers of rather large cork cells. The remainder of the gall is of moderately thin-walled parenchyma, the cells of which vary greatly in size. What is evidently a part of the palisade tissue of the leaf is still preserved in the upper part of the gall, just inside the epiderm and hypoderm (*e*). The remains of the old resin cavity of the leaf is shown at *r′*.

I have examined serial sections of a number of galls in about the same stage of development as the one shown in text fig. 1, and have always found essentially the same structures. It was not always the case that as good a transverse section of the stem inside the gall was seen as the one shown in the figure, as that depends on the plane through which the sections are cut, and is largely a matter of chance. I was always able, however, to get enough in the sections to show that such a structure was present. The epidermis and hypodermis of the old leaf always appear, and usually some of the palisade tissue. The cork layer usually forms on the outside, but one gall was found in which it had started to form below the periphery, cutting off some of the parenchyma. Stages between those shown in fig. 1 and text fig. 1, show that the tissue towards the base of the leaf first becomes involved in gall formation. The tissue towards the base may be greatly altered while that at the apex is still normal. The resin cavity may become very much elongated so that it appears at a higher level in the gall than it would in the normal leaf.

After having found a distinct stem structure in the young galls it is interesting to see what becomes of it in older galls. Fig. 3 is a diagrammatic drawing of a cross section made near the base of a gall near where the stem enters it. The stem has not become entirely enclosed by gall tissue at this point as a portion of the cork of the stem is still shown at *k*. The secondary bark tissue preserves many of its normal characters. The bast fibers occur in concentric rings, and there are sieve tubes and parenchyma layers between them. The bast rings are not continuous, however, as some of the fibers have been converted into parenchyma cells, a condition not dissimilar to what De Lamarlière (3) describes for the galls of *Gymnosporangium clavariaeforme* on stems of *Juniperus communis*. Bast fibers are entirely absent on the upper left side of the figure, while on the lower left side they are turned over nearly at right angles to their usual upright position. Occasional bast fibers are formed in the layers where normally only sieve tubes and parenchyma are developed. This is evidently not due to fibers being pushed out of place as they may occur where the bast rings are unbroken (see upper right side of figure).

The structure of the xylem is nearly normal except towards the upper side of the figure. The tracheids are here turned over more or less, and two multiseriate rays have formed in the wood.

There is not much change in the woody portion of the cylinder for some distance farther in from the section shown in fig. 3. Two projections appear after a time which develop into the condition shown in fig. 4. A large pith has developed in the center and two branches extend above and below. The one in the upper part of the figure is quite regular and presents many of the structures of a stem. A pith in the center is surrounded by wood in which there are rays extending outward into the somewhat modified secondary bark tissue (*b*) in which there are a few bast fibers distributed. The branch, which extends off on the lower side, is less regular, and soon breaks up into irregularly running strands of tracheids. The only parts which preserve a transverse stem structure are to the right and left of the center of the figure. There are a few wedges of xylem here which are separated by rays which are sometimes broader at the inner ends of the wedges. There are strands of tracheids running away from the central portion which are much bent and twisted. They extend in various directions. Some of them have tissue similar to the secondary bark of a normal stem, so they probably represent branches from the main central stem of the gall, but very much distorted and broken up. The tracheids which compose the irregular strands of vascular tissue usually have scalariform pits in their walls. The thickenings between the pits are often so slender as to give the appearance of spiral tracheids.

In addition to the irregular strands of tracheids that have just been mentioned, peculiar stem-like structures occur in the gall. These often present a true transverse stem structure so there can be no mistake about their being stems. As the origin of these is better shown in the next species to be considered, they will be taken up in that connection. Two of these are shown at *s*, in figs. 4 and 5. They are much more irregular in structure here than is often the case.

By further breaking up of the central cylinder deeper in the gall, a condition is finally reached in which there is nothing left but irregularly running strands of fibrovascular tissue. This condition is shown rather diagrammatically in fig. 5. All semblance of a transverse stem structure has disappeared, except towards the lower left side of the figure, and in two small areas in other places. The strands have become so twisted, in the central part of the figure, that the modified secondary bark tissue lies towards the center. Strands of tracheids sometimes surround rather broad ray-like masses of parenchyma as is shown in the upper part of the figure. From the central body, as figured, strands of tracheids radiate outward towards the periphery of the gall.

Sanford (8) makes the statement that there is but little distinction between xylem and phloem in the smaller bundles of the gall. The tracheids in the smaller bundles often show less lignification than those of the larger bundles, so that it is often difficult to differentiate sharply the tissues by staining. It is usually possible by careful staining, however, to show that certain of the cells are slightly lignified and have scalariform pits in their walls. Furthermore, elongated parenchyma cells usually accompany these in such a relation that one may assume that they are phloem cells, or cells that perform a similar function. Cells sometimes occur which are part parenchyma and part tracheid. They occur quite commonly in the gnarl-like complexes of cells in various places. As they are shown better in the next species, they will be considered further in that connection.

After having considered stages in the breaking up of the stem in the gall as seen in transverse section, a longitudinal section will now be considered. Such a section is shown diagrammatically through the basal portion of a mature gall in fig. 6. The central cylinder of the stem which bears the gall is shown at *c*, which continues off at the upper left side of the figure. The two branches to the right constitute the central cylinder which enters the gall. This cylinder has a very broad pith (*p*) which begins very suddenly near where it joins the main stem. The bundles on each side of the pith have a tissue similar to secondary bark (*b*), in which there are strands of bast fibers. Rays occur among the tracheids of both bundles, and continue into the secondary bark as shown by the cross lines in the drawing. A portion of the old leaf is still attached to the lower part of the gall, some of the tissue of which seems still to be unaltered. The epidermis and hypodermis are shown at *e*, and the resin cavity at *r*, surrounded by the more or less modified parenchyma of the leaf. Immediately above the resin cavity there is a strand of tracheids with bar-like thickenings (*l*), such as always accompany the leaf-trace bundles. This branches and joins the base of the central cylinder entering the gall at about the same place that the leaf-trace bundle joins the central cylinder in the young gall shown in fig. 1. There can be no doubt about this being a portion of a leaf-trace bundle especially as another leaf trace (*l'*) leaves the central cylinder just opposite. There is an irregular mass of tracheids just above this strand, but whether or not it is made up of tracheids from the leaf trace, or is a branch from the main stem, I could not determine. The leaf trace bundle, in addition to the other bundles, is thus accounted for in a very young as well as in an old gall; so there can be no further doubt that the other bundles are derived from a stem. They are not leaf-trace bundles which have assumed the structure of a stem as was stated by Sanford.

The remainder of the gall tissue consists of loosely arranged parenchyma cells which are surrounded on the outside by layers of cork cells. Except near the central cylinder, the parenchyma cells for the most part are not strikingly larger in the older gall than they are in the younger gall (shown in text fig. 1). Starch as well as droplets of oil occurs abundantly in many of the cells.

Since this article was sent away for publication a paper has appeared by Reed and Crabill (12) in which the anatomy of the gall of *Gymnosporangium juniperi-virginianae* is briefly considered. These authors regard this gall as arising from nothing more than an hypertrophied leaf, and that its fibrovascular system is a modified continuation of the fibrovascular system of the leaf.

From the descriptions and figures which have been given in the preceding pages, it seems evident that these authors have been mistaken in their interpretations. The diagrammatic drawing of a longitudinal section of a young gall and of a branch, which they show in their fig. 4, is probably of a stage intermediate between the galls I have figured in fig. 1, and text fig. 1. These authors have seemingly failed to find a leaf-trace bundle in addition to what they have shown, and have interpreted the fibrovascular system as a modified leaf trace. A section cut at right angles to the one shown in their figure would probably reveal the fact that this system has the structure of a stem and is in no way a leaf bundle.

GYMNOSPORANGIUM GLOBOSUM ON JUNIPERUS VIRGINIANA.

The relation of the younger galls of *G. globosum* Farl. to stem and leaf is very similar to that of *G. juniperi-virginianae*, considered earlier in this article. In fact the similarity is so great that it is practically impossible to distinguish the two with any degree of certainty until the sori have formed. Cross sections of the younger galls have essentially the same structure as galls of similar size which are caused by *G. juniperi-virginianae* (text fig. 1). There is this exception, however, that the strands of tracheids given off from the stem in the gall, which correspond to the two strands at the right of the resin cavity (*r′* in the above mentioned figure), are separated by a very broad band of parenchyma. This condition is to be expected from what is usually found in the older galls caused by this species of Gymnosporangium.

The woody cylinder in older galls presents two entirely different types as far as was shown by the material studied. The more common of these types will be considered first. A cross section of an oldegall, made near where the gall joins the main stem, is shown diagrammatically in fig. 8. The relative position of this section in the gall is about the same as the section of *G. juniperi-virginianae* shown in fig. 3. The magnification of this figure is much higher than is that of fig. 8, so that the central cylinder is much wider at the start in the *globosum* gall. What is evidently very much modified tissue of the secondary bark is shown at *b*, which is not well differentiated on the right and left sides of the figure. Bast fibers are fewer in number as can be seen by comparing the two figures just mentioned. A median longitudinal section of a portion of the stem bearing the gall is shown at *c*, the pith being the stippled portion in the center. Tracheids radiate outward above and below, and in the center of the figure they take an irregular course next to the secondary bark tissue. Sections taken a little deeper often show strands of tracheids running through the modified pith tissue (fig. 9) which often surround broad, ray-like masses of parenchyma. They may continue for some time and then disappear resulting in the condition shown in fig. 9. Secondary bark tissue is fairly well differentiated in this section and can be seen entirely around the cylinder. The tracheids take a very irregular course inside of this, but in places there are wedges of xylem which show a true transverse structure. They are shown by the triangular area covered with cross lines in fig. 9, and one is shown under high magnification in fig. 12. This wedge presents what appears to be three distinct rings of growth, as there are three bands each of spring and summer wood alternating with each other. Whether or not these are true annual rings I do not know. As this gall is perennial in growth, and as secondary thickening takes place in both of the galls being considered in this article, it is not unreasonable to suppose that they are true rings of growth. If they are rings of growth they are better developed, where they occur, than in the galls of *G. juniperinum* where, according to Wörnle (11), growth rings are poorly marked.

The woody cylinder widens deeper in the gall as can be seen by comparing figs. 8 and 9. The greatest diameter in the gall figured is nearly 5 mm., but galls were examined in which it was more than 8 mm. The cylinder finally breaks up and branches out in the gall, but preserves a semblance of a stem structure much deeper than in the gall of *G. juniperi-virginianae* previously considered.

The origin of secondary stem structures in the gall is shown in figs. 13, 14, and 15. A portion of the woody cylinder (fig. 9), pushes outward in the manner shown in fig. 13. This projection becomes larger and somewhat expanded at the apex while it contracts at the base (fig. 14). Strands of tracheids, surrounding broad, ray-like masses of parenchyma, often fill up the constricted portion as is shown in the figure. After a time the projection becomes separated from the central cylinder, or nearly so (fig. 15), after which it assumes the character of the main woody cylinder from which it arose, except that it is smaller in size.

I have been unable to determine the cause of these accessory stems, but, arising as the gall does from a transformed axillary bud, it is not unreasonable to suppose that latent properties for bud formation, inherent in it, are stimulated to activity through the action of the fungus.

A longitudinal section through this type of gall is shown in fig. 10. The section figured was made at right angles to the ones shown in figs. 8 and 9. A portion of the stem which bears the gall is shown at *c*. Strands of tracheids go off from this on the right and left sides of the figure. This is surrounded by gall parenchyma (*gp*) which is surrounded on the outside by cork (*k*).

In the second type to be considered, the woody cylinder preserves more of its normal structure at the point of entrance into the gall, and is more like the galls of *G. juniperi-virginianae* in this respect than in the type just described. The woody cylinder is not greatly altered at first, but there is a considerable production of parenchyma at the expense of the tracheids. Many of the parenchyma cells have the form of tracheids when seen in cross section, but the walls are unlignified and protoplasm is present in them. Broad rays are formed which cut the cylinder into wedge-like masses similar to the one shown in fig. 12. Bast fibers occur but seldom in the secondary bark tissue, similar in this respect to the first of the type of *globosum* gall described.

A short distance beyond the point of entrance of the stem into the gall, the pith begins to enlarge and the rays broaden, thus pushing the xylem wedges farther apart. This process is attended with more or less displacement of tracheids in sectors of the cylinder. The enlargement of the pith and other abnormalities continue, until deep in the gall the woody cylinder assumes a form very similar to that shown in fig. 9, where most of the groups of tracheids extend in various directions. A few of them still remain in their normal position and appear as the xylem wedges, mentioned several times before in this article. Sooner or later the various groups of tracheids diffuse outward into the gall and all semblance of a central stem structure is lost.

Gnarl-like complexes of tracheids and parenchyma cells occur in both of the types of globosum galls described. The one shown in fig. 11 consists of a mass of cells wound around a parenchyma center and is not dissimilar to the "Knaueln" described by Mäule (7) from traumatic wood. Cells which are transitional between tracheids and parenchyma are shown in this figure. One end of such a cell usually has a lignified wall in which there are scalariform pits, while at the other end the wall is of cellulose and a protoplasmic content is present Transitional cells of this nature have been reported in several other kinds of pathological plant tissue. Mäule (7) has found them in the traumatic wood of *Abies cephalonica*; Smith (9) has described and figured somewhat similar cells in the tumor strand of crown gall on the tobacco stem; and the writer has found such cells to be present in the galls of *Peridermium cerebrum* on *Pinus Banksiana* (see Stewart (10)). Such cells have probably been reported in still other kinds of abnormal plant tissue. They seem to have quite a wide distribution.

METHODS

In preparing material for study, the galls were embedded in celloidin as there was too much lignified tissue present to get good section when embedded in parafin. The sections were usually mounted in series and stained with safranin. Either Delafield's hematoxylin or "licht Grün" was used as a counter stain. The drawings were made with a Spencer Delineascope and are diagrammatic for the most part. In order to cover wide enough field to show all of the structures desired, a low magnification was necessary. Great detail was impossible under such circumstances.

SUMMARY

1. *Gymnosporangium juniperi-virginianae* and *G. globosum* cause the formation of large galls on the younger branches of *Juniperus virginiana.*

2. The galls arise from the axils of the leaves and are evidently transformed axillary buds.

3. Young galls have two distinct fibrovascular systems, one of which is a leaf-trace bundle, and the other a stem.

4. The more or less modified stem which enters the base of the older galls gradually breaks up and radiates outward, deeper in the gall tissue.

5. Leaf tissue is also involved in gall formation, and remains of it are usually to be found adhering to the older galls.

6. Normal stems sometimes appear to have grown out from the surface of the older galls.

7. Accessory stem structures occur, which probably originate by a branching of the main stem in the gall.

8. Broad, ray-like masses of parenchyma, surrounded by tracheids, are of rather common occurrence.

9. Irregularly twisted masses of fibrovascular tissue occur which are similar in many respects to like structures in traumatic wood.

10. Cells which are transitional between parenchyma and tracheids are quite abundant.

11. The irregularly running bundles in the gall are composed largely of scalariform tracheids.

12. The statements in the above summary apply in a general way to both the galls considered in this article.

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SUMMARY OF LITERATURE CITED

1. **Coons, G. H.** Some Investigations on the Cedar Rust Fungus, Gymnosporangium juniperi-virginianae. Ann. Rep. Neb. Exp. Sta. 25: 217–245. pls. 1–5. 1912.
2. **De Bary, A.** Comparative Anatomy of the Vegetative Organs of Phanerogams and Ferns. 659. 1884.
3. **De Lamarlière, G.** Sur les Mycocécidies des Gymnosporangium. Ann. Sci. Nat. Bot. IX 2: 313–350, pls. 9–12. 1905.
4. **Engler, A. & Prantl, K.** Die Naturlichen Pflanzenfamilien. 1^1: 570. 1900.
5. **Heald, E. D.** The Life History of the Cedar Rust Fungus Gymnosporangium juniperi-virginianae Schw. Ann. Rep. Neb. Agric. Exp. Sta. 22: 105–113, pls. 1–13. 1909.
6. **Kern, F. D.** A Biologic and Taxonomic Study of the genus Gymnosporangium. Bull. N. Y. Bot. Gard. 7: 391–494, pls. 151–161. 1909–1911.
7. **Mäule, C.** Faserverlauf im Wundholz. Bibl. Bot. Heft 33: 1–32, pls. 1–2. 1895.
8. **Sanford, E.** Microscopical Anatomy of the Common Cedar Apple (Gymnosporangium macropus). Annals of Botany 1: 263–268, pl. 13. 1888.

9. **Smith, E. F.** The Structure and Development of Crown Gall. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 255, pp. 1–60, pls. 1–109. 1912.

10. **Stewart, A.** Notes on the Anatomy of Peridermium Galls I. Amer. Jour. Bot. (In press).

11. **Wörnle, P.** Anatomische Untersuchung der durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forstl. Natürw. Zeitsch. **3**: 68–84, 129–172. 1894.

12. **Reed, Howard S. and Crabill, G. E.** The Cedar Rust Disease of Apples Caused by Gymnosporangium juniperi-virginianae Schw. Tech. Bull. 9, Virginia Agricultural Experiment Station. 1915.

EXPLANATION OF PLATES XV AND XVI

PLATE XV

Gymnosporangium juniperi-virginianae on *Juniperus virginiana*

FIG. 1. Diagrammatic drawing of a longitudinal section through a very young gall and of the stem that bears it. *C*, central cylinder of stem. *E*, epidermis and hypodermis of leaf. *K*, cork layer. *L*, leaf trace bundles. *R*, resin cavity in leaf; × 42.

FIG. 2. Diagrammatic drawing of a longitudinal section of a portion of a young juniper stem and an axillary bud. *Bd*, axillary bud. Other lettering same as in figure 1; × 42.

FIG. 3. Diagrammatic drawing of a cross section of a stem near where it enters the base of the gall. *B*, tissue of secondary bark. *K*, cork layer; × 42.

FIG. 4. Similar to fig. 3, but taken from a section deeper in the gall. *B*, modified tissue of secondary bark. *P*, pith. *S*, accessory stem structure in the gall; × 42.

FIG. 5. Similar to fig. 4, but taken from a section still deeper in the gall where the stem has become almost entirely disorganized. Lettering same as in fig. 4; × 42.

FIG. 6. Diagrammatic drawing of a longitudinal section through the basal portion of an older gall and of the stem that bears it. *B*, modified tissue of secondary bark. *C*, central cylinder of main stem bearing gall. *E*, epidermis and hypodermis of leaf which has become involved in gall formation. *L*, leaf-trace bundle. *P*, pith of central cylinder inside gall. *R*, resin cavity in leaf; × 42.

FIG. 7. Apparently normal branch growing from gall. *B*, more or less modified tissue of secondary bark. *K*, cork layer surrounding gall. *R*, resin cavity in leaf; × 14.

PLATE XVI

Gymnosporangium globosum on *Juniperus virginiana*

FIG. 8. Diagrammatic drawing of a cross section of the central cylinder near where it first enters the gall. *B*, modified tissue of secondary bark. *C*, portion of central cylinder of stem that bears the gall. *Gp*, gall parenchyma which entirely surrounds the parts figured; × 14.

FIG. 9. Similar to fig. 8, but from a deeper section in the gall. *P*, pith. Other lettering same as in fig. 8; × 14.

FIG. 10. Diagrammatic drawing of a longitudinal section through a gall made at right angles to the ones shown in fig. 8 and 9. The figure shows a longitudinal view of the central cylinder at its point of entrance into the gall. *K*, cork layer. Other lettering same as in figures 8 and 9; × 14.

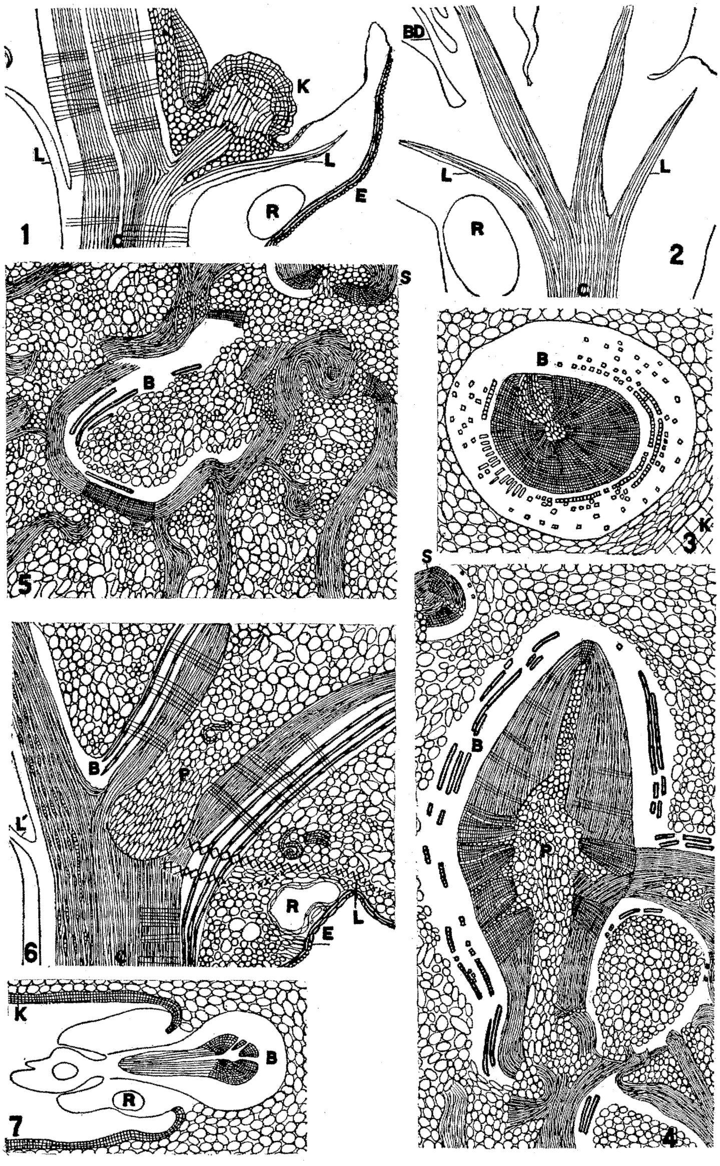
FIG. 11. Drawing of one of the gnarl-like complexes of cells in the gall, showing scalariform tracheids, parenchyma cells, and cells which are transitional between tracheids and parenchyma; × 200.

FIG. 12. Drawing of a cross section of one of the xylem wedges in the gall with three rings of growth. Similar wedges are shown diagrammatically in figs. 9, 13, 14, and 15; × 200.

FIG. 13. Pushing outward of a portion of the woody part of the central cylinder in the gall preparatory to forming an accessory stem structure; × 14.

FIG. 14. Similar to fig. 13, but showing a somewhat later stage; × 14.

FIG. 15. Accessory stem structure near point of departure from main central cylinder in gall; × 14.



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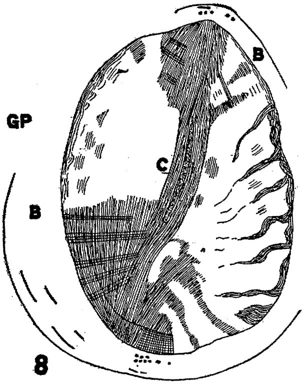

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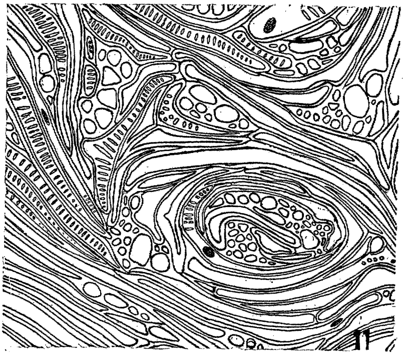

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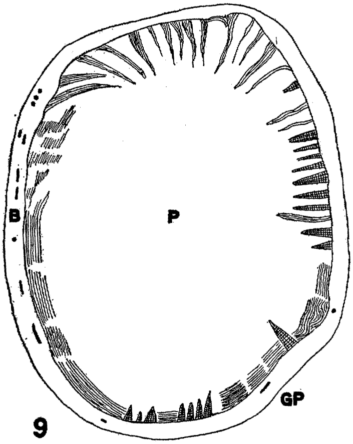

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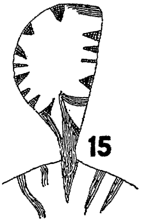

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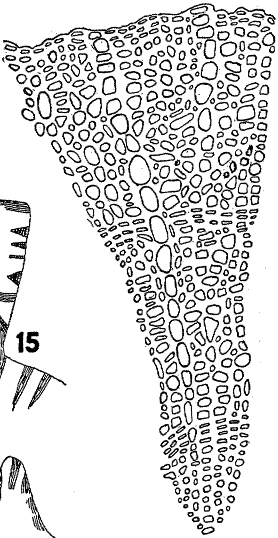

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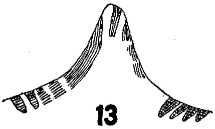

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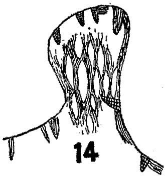

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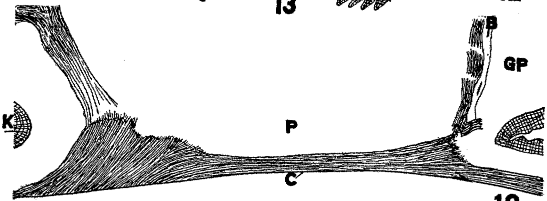

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